

posts are held by men. It isn't always easy for young women to have social confidence necessary to not only engage but stand out in their respective scientific communities and the competition for faculty positions is stiff. That being said, I think a lot has changed for the better in the last 20 years that I have been in science and the climate is still improving. A second challenge that women face is the fact that they are at a fitness disadvantage if they opt for a scientific career in spite of measures to overturn this. If you consider that most people do not reach tenure until their late 30s or early 40s — it is easy to see how this presents a disadvantage for women, who are most fecund before the age of 35. Further, babies and the careers of early investigators both require a lot of investment.....I guess you get the picture. My male colleagues do not face the same trade-offs between family and career. There are ways around it for women, but they aren't simple. Perhaps society will eventually make it easier for young women to do both. This will depend in part on how much we value having women in science.

**What's the next big question in your field?** I'm most interested in the neural basis of learning and memory. Bees are a great model for studying this because adult workers are excellent at learning to associate scent, visual and even tactile cues with food. For me, one of the most exciting areas of research in this field is to identify how state influences learning and memory, and I think that studying it in invertebrate models presents a great opportunity to get at the fundamental principles. For example, my friends and I recently showed that decision-making in bees is influenced by 'emotional' state. Whether or not bees have a genuine correlate of emotion is debatable, but state definitely alters their decision-making.

Drug and alcohol addiction claims the lives of so many people and causes a myriad of social problems. I think that one of the world's greatest challenges at the moment is to find ways to combat addiction. As scientists, we can help by identifying the neural basis of addiction with the aim of developing therapeutic and pharmacological interventions. I believe that understanding addiction will likewise reveal fundamental

principles about the way the brain functions — both in terms of what we understand about specific circuits, such as those involved in reward learning and memory — but also as a complex living organ whose activity is modulated by short- and long-term changes in state. Who knows if we can get the much smaller brains of invertebrates addicted to substances? There is some intriguing research on fruit flies that suggests this is possible. If we cannot, that is equally interesting.

**What do you advise a student who doesn't know what topic in biology to specialize in?** I would first say: read more. Start reading through the high impact general journals regularly, and make note both of things that interest you and who is doing them. Think about what you like to spend your time doing — is it being outdoors or spending time at the bench? What do you foresee yourself doing in 5 or 10 years? Talk to students and postdocs at your university, and find out how they spend their time and what their opportunities are. It is also useful to look at what kinds of jobs are offered to people in the field you are attracted to (there may not be many advertisements for behavioural ecologists studying tigers). Find an active lab that is publishing in the field that interests you, read their papers, and don't be afraid to write to the lab head to ask what kinds of projects you could get involved in.

**What do you like most about your job?** The opportunity to spend my time pursuing what is intellectually interesting to me is by far the best thing about being an academic. I love learning and that's a real bonus for me. I also love looking at and interpreting data. It can be extremely rewarding to develop a hypothesis and see how it pans out. After one has spent time and effort collecting data, for me there is real joy in using statistics to test a hypothesis: I still get a thrill when I run a stats program to analyse data from an experiment. If anything, my Achilles heel is knowing when to stop collecting and analysing, and when to start writing it up!

Centre for Behaviour and Evolution, Institute of Neuroscience, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK.  
E-mail: [jeri.wright@ncl.ac.uk](mailto:jeri.wright@ncl.ac.uk)

## Quick guides

### *Equisetum*

Anne Knowlton

**What is *Equisetum*?** *Equisetum*, a genus whose species are collectively known as horsetails, are the living descendants of giant prehistoric trees that once dominated the Earth. These ancient giants remain with us today in the form of coal. The living species of *Equisetum* offer biologists a peek into the history and evolution of vascular land plants.

*Equisetum* is the single extant genus of a class of anciently evolved land plants. Fossils of the ancient giants are found dating back to the Devonian, and in the late Devonian and Carboniferous periods, the world's forests were dominated by the calamites — huge tree-like horsetails that reached heights of up to 18 meters. These ancient forests were a far cry from forests in today's world — many large land animals had not evolved by this point, and fossil records indicate that giant insects had the run of the place! The calamite forests were so rich that they eventually formed the world's large coal deposits. As the climate grew drastically drier and colder in the Permian, concomitant with a change in atmospheric oxygen content, the giant calamites eventually died out, leaving only the herbaceous genus *Equisetum* in modern times.

*Equisetum* species are almost identical to the ancient calamites in morphology, earning *Equisetum* the label of 'living fossils'. Horsetails are found in various habitats around the world, though they usually prefer wet, swampy areas. Although there are examples of 'giant' horsetails (e.g. one Mexican species has been reported to reach heights of 8 meters), most horsetails are much smaller than their ancestors, and are usually around 1 meter or shorter.

**How would I know a horsetail if I saw one?** *Equisetum* have a very distinctive appearance, growing in dense clusters as jointed, photosynthetic stems (Figure 1A). These stems are sometimes branched, with whorls of branches appearing at the joints between

segments. Horsetails have very small, scale-like leaves, called microphylls, which are usually non-photosynthetic and are hardly noticeable in some species. The internodes of the stems of horsetails contain a hollow pith, around which smaller hollow canals — called vallicular and carinal canals — are arranged, in close association with the xylem and phloem. One of the most recognizable features of horsetails is their ribbed stems, which are reinforced with silica deposits in the epidermal cells, giving the stem a very rough texture. The stems arise as branches from an underground rhizome. Although the stems tend to die off during winter or in the dry season, the rhizome is perennial. In fact, since removal of horsetails from a particular area requires the removal of the entire rhizome, horsetails can be very hard to eradicate, and are considered pests in some places.

#### ***How do horsetails reproduce?***

Horsetails, like their close relatives the ferns, are evolutionarily ancient plants and don't produce seeds to protect and nourish their offspring. The sporophyte, or diploid, phase of the *Equisetum* life cycle is the dominant one and is represented by the herbaceous stems described above. Structures called strobili at the tips of fertile shoots house the developing haploid spores. In some cases, the fertile shoots look

identical to the vegetative shoots (save for the strobili), but in others, the fertile shoots aren't photosynthetic at all and appear as white or brown shoots (Figure 1B). When the spores mature, specialized structures called elaters expand and contract during daily cycles of high and low moisture, helping to fling the spores from the plant.

The bright green spores germinate, and the gametophyte, or haploid, phase of the life cycle begins. The photosynthetic gametophytes of *Equisetum* are small, flat, lobed structures (only a few millimeters wide), with rhizoids attaching them to the substratum. Eggs and sperm are produced on different lobes of the gametophyte. The sperm are flagellated and require water to swim to and fertilize the eggs, making a moist habitat essential for reproduction. Once fertilization is successful, a new diploid sporophyte will develop.

#### ***What can horsetails tell us about the evolution of vascular plants?***

Though they are quite anomalous in form — most land plants have highly developed leaves to maximize photosynthetic surface area, while *Equisetum* leaves are practically vestigial as photosynthetic organs — horsetails, as well as the other seedless vascular plants, evolved at a time when the Earth was

quite different. At the time when plants were beginning to colonize land, the climate was quite tropical, and ancient land plants had no need to develop ways to cope with water shortages. As a result, all of the 'primitive' vascular plants (seedless plants) have their reproductive cycles intimately dependent on water availability. As discussed in the section above, the gametophytes of these species, and of the other seedless vascular plants, produce flagellated sperm that require water to swim to the eggs. Once the climate turned drier and colder in many parts of the globe, and as atmospheric oxygen gradually rose, these ancient giants died out, and evolution of modern-day vascular seed-bearing plants took off in earnest — along the way developing different modes of reproduction, relying on wind and animal pollinators instead of on water. In the more recently evolved gymnosperms and angiosperms, the gametophyte stage of the life cycle has been reduced to a very small number of cells, which rarely ever even make contact with the ground. The angiosperms also evolved protective seeds, providing nutrients for the young embryo, allowing development and germination of offspring even in otherwise unfavorable conditions.

The global climate change, along with concomitant changes in atmospheric content, resulted

A



B

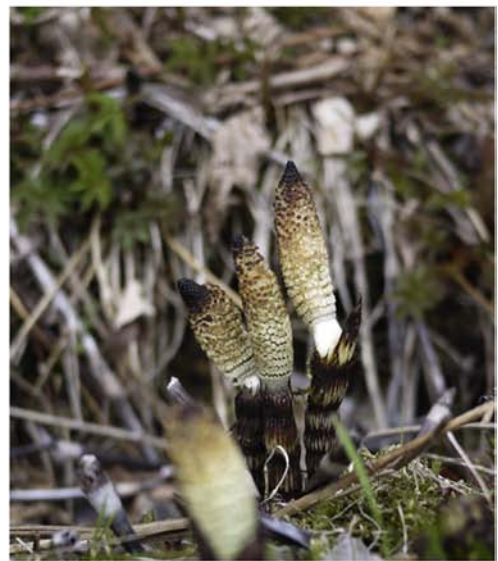


Figure 1. *Equisetum*.

(A) Vegetative shoots of horsetails. Photograph courtesy of Wikimedia Commons. (B) Fertile *Equisetum* shoots emerging from the ground in spring, containing spores within the strobili at the top of the shoots. Photograph courtesy of Andreas Wolf.

in a nearly complete overthrow of the seedless vascular plants, which once dominated the planet. The modern-day descendants of these giants, still dependent on water for half of their life cycle, are almost exclusively confined to swampy or tropical habitats. *Equisetum*, with their highly proliferative and resilient rhizomes, are more versatile than many species and can be found in various environments.

#### **How do humans use *Equisetum*?**

In many cultures, the rough stems of horsetails are dried and used to scour and polish metal pots and pans, earning them the name 'scouring rush' in some parts of the world. In addition, traditional Japanese woodworkers use dried *Equisetum* as a type of extra-fine sandpaper. Since *Equisetum* species can be found all over the globe (except Australasia), they have made their way into the traditional medicine practices of various cultures, dating back to ancient Greek and Roman times. The silica in the stems of horsetails is thought to aid in osteoporosis prevention, while extracts from horsetails are used for many different reasons, including as a diuretic, and as a source of natural antioxidants. Very few studies, though, have been performed to weigh the merit of these alternative medical uses for the plant. Interestingly, livestock have been known to become ill and even die after eating large quantities of *Equisetum* — for this reason, and because most commercial pesticides kill only seed-bearing plants, horsetails are considered to be tricky pests in some areas.

#### **Where can I find out more?**

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Anne Knowlton is *Current Biology's* Assistant Editor.  
E-mail: [aknowlton@cell.com](mailto:aknowlton@cell.com)

## **Sense of agency**

Patrick Haggard<sup>1</sup>  
and Valerian Chambon<sup>1,2</sup>

**What is the sense of agency?** The term 'sense of agency' refers to the experience of controlling one's own actions, and, through them, events in the outside world. Most of us have the feeling that we are in control of what we are doing most of the time: this is the normal sense of agency.

**Why is it important?** Some many mental illnesses involve abnormalities of agency: psychotic patients sometimes report that their actions are not their own, but are imposed on them by some other agent, while depressed patients often experience helplessness and loss of agency. Sense of agency also plays an important role in society generally, because it is central to the idea of responsibility for our own actions. In many countries, the law requires that a person be aware of the consequences of their actions, if they are to be found guilty of a crime.

**How can sense of agency be studied scientifically?** Despite its importance, sense of agency has proved difficult to study scientifically. Loss of agency, for example when one is driving a car that suddenly malfunctions, is a salient, and dramatic experience. But the normal flow of action and control forms a continuous, thin background to consciousness, rather than a specific, identifiable experience. Psychology and neuroscience have struggled to measure sense of agency. Most studies have used explicit agency attribution tasks, in which a person judges whether they did or did not cause a specific event. One experimental paradigm, for example, involves participants moving a joystick, while watching video feedback. They judge whether they caused the joystick movement shown on the video or not, equivalent to evaluating the truth or falsity of the proposition "I did that". These studies have shown that spatial and temporal contiguity between one's own and the observed movement are the major cues for self-attributing agency; however, they say little about the *phenomenology* or experience of

agency: that is, what it feels like to be in control of the image viewed on the screen, as opposed to out of control.

**What brain computations underlie sense of agency?** The experiments described above suggest the brain computes agency by predicting the consequences of current actions, and comparing these predictions to actual outcomes (Figure 1A). In the example above, knowing how one moves the joystick allows one to predict the visual feedback. If the video feedback matches the prediction, then it follows that "I did that". If there is no match, then the visual feedback must have another cause. This account is based on the computations used to monitor and adjust motor commands in a popular computational framework for action control, leading to the suggestion that sense of agency is simply the normal operation of the goal-directed action system (Farrer *et al.* 2008). In this framework, agency is computed by comparing a prospective signal (the intention or command to achieve the goal) and a retrospective signal (the actual feedback or outcome of action). An internal forward model uses a copy of the current motor command to predict the feedback that the action will produce. If the comparison between predicted and actual feedback generates no error, then "I did that".

Brain imaging studies of such tasks have not found any clear positive correlate of agency, but routinely show activation of the angular gyrus in the parietal cortex in situations of non-agency. Angular gyrus activation increases proportionately as the subjective sense of agency decreases. This brain area may therefore either house the comparator, or receive the error signals transmitted by a comparator located somewhere else in the brain. These studies suggest a strong link between sense of agency and error-monitoring in the motor control system, but they leave two important questions unanswered. First, why do we have a positive sense of agency, in addition to the negative sense of non-agency that occurs when the outcome of an action is not as predicted? Second, what experience is there prior to receiving delayed feedback about action outcomes: could an experience similar to agency